The role of forage quantity and quality in the migration and diet of a northern ungulate during their neonatal period

by

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Abstract

Migration has evolved as a strategy to maximize survival and reproductive success, driven by the search for better resources and predator avoidance. For ungulates at high latitudes, the search for higher quality and more abundant forage has been proposed as one of the best explanations of seasonal migrations. However, responses vary among populations, species and ecosystems. In this study we focus on the Ronald Lake wood bison herd (RLBH) in northeastern Alberta that annually migrates outside of its core range to an upland meadow complex at the base of the Birch Mountains. Reasons for this migration are unknown, however, the timing of the migration corresponds to the neonatal period in late spring during green up when females have a higher nutritional demand imposed by gestation and maternal care of neonates. Our goal was to understand how forage quantity (i.e., biomass) and quality (i.e., crude protein and metabolizable energy, ME) influence the migration and diet of this herd by comparing forage characteristics between their core and neonatal ranges. We found seasonal changes in the herd's diet, with a more graminoid-dominated diet during winter in the core range and a shrub and forb-dominated diet in the neonatal range and core ranges in late spring and through the summer respectively. Our findings also revealed that the neonatal range had significantly higher biomass ($p < 0.001$) of shrubs and forbs compared to the core range, being 1.7 and 3.8 times higher, respectively. The neonatal range also had more crude protein and ME ($p < 0.001$), being up to 3.0 and 3.7 times higher than the core range for shrubs and forbs respectively. Conversely, the core range had the highest biomass, crude protein, and ME ($p < 0.001$) for graminoids, although this forage group is not particularly important in their diet during their migration period. With the higher energy demands imposed on females during gestation and post-parturition, our results suggest that the herd's migration to the meadow complex with its higher quantity and quality of forage is important for female wood bison in the Ronald Lake range during this critical neonatal period.

Preface

This thesis is an original work by Sebastian Buitrago Gutierrez.

To date, no manuscript has been submitted for publication, but I plan to submit a version of this text for publication in *Ecology and Evolution* with co-authors of M.A. Edwards (co-supervisor), L.J. Hecker (collaborator), and S.E. Nielsen (supervisor). For this manuscript, L.J. Hecker conducted fieldwork, collected data, and provided input on writing. S. Buitrago Gutierrez co-designed the study, conducted fieldwork, collected data, conducted analyses, and wrote the manuscript. M.A. Edwards and S.E. Nielsen designed the study, supervised the research, and provided feedback on analyses and writing.

Dedication

I dedicate this thesis to my father, Jesús María Buitrago Flórez. Your words and instructions have always encouraged me to pursue my dreams and to not fail in the process. My passion for animals and nature is rooted in the life experiences we have shared in our lifespans.

I would also like to dedicate this thesis to my mother, Lucero Gutiérrez Ramírez. Without your love, support, and words this journey would have not been possible. Your personal example has always inspired me to keep moving forward.

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Table of Contents

List of tables

List of figures

List of appendices

Introduction

Migration has evolved as a strategy to balance predation and the spatio-temporal availability of resources, with the underlying principle that organisms distribute themselves to maximize their survival and reproductive success (Boyce, 1979; Orians, 1980; Fryxell and Sinclair, 1988). For large-bodied herbivores, migration is predominantly influenced by the search for higher quality and more abundant forage, particularly in temperate environments with marked seasonality (Fretwell, 1972; Dupke et al, 2017; Sigrist et al., 2022). When moving to a new location inside their home range, herbivores will trade-off between forage quantity and quality (McArthur and Pianka, 1966; Van der Wal et al., 2000). While high quantities of forage can improve short-term food intake, they also constrain the forage processing time due to a lower digestibility of highly fibrous materials (Spalinger and Hobbs, 1992; Wilmshurst et al., 1999). Therefore, to maximize their energy intake, individuals should search for new growth that is rich in nutrients but low in fiber (Fryxell, 1991). Tracking of the new nutrient-rich forage has been proposed as a key reason for seasonal migration in ungulates (McNaughton, 1985; Bischof et al., 2012; Aikens et al., 2017), although this may vary among populations, species, and ecosystems (Mysterud et al., 2011; Geremia et al., 2019; Laforge et al., 2020).

Forage nutritional value, particularly in terms of protein and energy, declines as the seasons progress, peaking during the spring growing season and steadily diminishing through summer and fall, reaching its lowest levels in winter (Van Soest, 1982; Langvatn and Hanley, 1993; Cook et al., 2016). Although graminoids, forbs, and shrubs all undergo these seasonal changes in quality, they all present a distinct nutrient composition (Lee, 2018) that ultimately influences their selection by ungulates. Graminoids generally contain higher levels of cellulose and hemicellulose (i.e. fiber), but lower levels of protein compared with shrubs and forbs (Robbins, 1993: Lee, 2018). Since energy is derived from the digestion of food components (i.e., protein, carbohydrates, fat), the lower digestibility of graminoids also limits the amount of energy they can provide to ungulates as a food item (Bliss, 1962; Robbins 1993). As a result, ungulates aiming to maximize their energy and protein intake are more likely to choose shrubs and forbs over graminoids.

Ungulates living in temperate environments, where seasonality exposes them to harsh weather conditions, typically exhibit high nutritional requirements while also having short periods to meet their needs (Lawler and White, 2003; Lovegrove, 2000; Strickland et al., 2005). This is particularly true for females, as gestation and lactation impose high protein and energetic demands (Thomas, 1971; Bowyer, 1984; Oftedal, 1985). Female ungulates can experience up to 50% and 215% increases in their energetic requirement while gestating and lactating, respectively, with the highest requirements occurring from late winter into mid-summer (Oftedal, 1985; Pekins et al., 1998). Since graminoids, which are high in fiber but low in protein, are the predominant source of food in winter, female ungulates should select for shrubs and forbs to meet their higher demands during spring and summer when the highly nutritious new growthbecomes available (White, 1983; Gordon & Illius, 1989; Lee, 2018).

The Ronald Lake wood bison (*Bison bison athabascae* Rhoads, 1898) herd (RLBH) is a small ungulate population (~270 individuals) located in northeastern Alberta, Canada. The herd is of high conservation value due to their disease-free status, distinctive genetic structure among Alberta's wood bison herds, and because of their cultural importance to regional Indigenous communities (Ball et al., 2016; Nishi, 2017). They are listed as "Threatened" under the Alberta Wildlife Act (Government of Alberta, 2023) and Canada's Species at Risk Act (Government of Canada, 2023), and have been the focus of research and management during the last decade due to oil sand exploration and proposed oil sands mining that overlaps part of the herd's core range (Sheppard et al., 2014; Hecker et al., 2021, 2023). The herd exhibits an annual migration (~28-km) in late spring/early summer (mid to late-May) to a large (82 ha) upland meadow complex west of their core range, near the northeastern base of the Birch Mountains (Tan et al., 2014). Small groups typically move to this meadow complex using a southern corridor, and they synchronously migrate back about 5 to 6 weeks later (late-June to early-July) using a northern corridor. Reasons for this migration are unknown, however, the timing corresponds with the neonatal period and shortly after the start of spring green up. Understanding the factors that influence the herd's seasonal migration during this critical period is crucial for identifying essential seasonal habitats for nutritional replenishment and determining potential population-limiting factors.

Here we focus on understanding what factors influence the seasonal migration of the RLBH from the core range to the spring neonatal range during the neonatal period. Dewart (2023) found that predation on the RLBH by wolves (*Canis lupus*) was limited, therefore we concentrated on examining bottom-up differences in forage quantity and quality between the seasonal ranges. Specifically, our objectives were two-fold: 1) compare diets between the core and neonatal ranges; and 2) test whether forage quantity and quality differ between the two ranges. We hypothesized that: (1) the herd's diet will be mainly composed of graminoids in their core range during winter, as they are the most available forage. In the neonatal range during early spring to early summer, their diet should shift to new shrub and forb growth due to its high nutritional value, and by the end of summer in the core range, the diet should be more balanced among shrubs, forbs and graminoids; (2) given the higher nutritional demands during the neonatal period, we expect that the neonatal range will have greater quantity (i.e., biomass) and quality (i.e., protein and energy) of forage compared with the core range, thus helping to explain the migratory behavior. This work builds on previous studies of the herd's habitat, but with a focus on the neonatal period and the goal of informing conservation and management decisions on critical habitat for the herd during this brief, but important period.

Methods

Study area

The RLBH occupies an area centered on Ronald Lake in northeastern Alberta, Canada. Our study area encompasses the RLBH core home range and their neonatal range, extending from the southeastern corner of Wood Buffalo National Park in the north, south into Alberta's oil sands region, east to the Athabasca River and west to the Birch Mountains (Figure 1a; DeMars et al., 2020). Elevation ranges from 240 to 300 m above sea level with the climate characterized as northern continental, having short and warm summers, and long and cold winters (Downing and Pettapiece, 2006). The study area is located within the Boreal Plains Ecoregion and presents a mosaic of ecosystems dominated by deciduous, coniferous, and mixedwood forest in the uplands, with marshes and peatlands in the lowlands (Downing and Pettapiece, 2006). While all the ecosystems mentioned can be found in the core range, the neonatal range is characterized by a long-continuous (~2-km length by ~0.5-km width) upland shrubby meadow and surrounded by upland deciduous and mixed forests, with little coverage of lowland ecosystems (Figure 1b). In the core range, forests are dominated by trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and jack pine (*Pinus banksiana*), and wetlands and marshes are abundant in sedges (*Carex* spp.) and grasses from the Poaceae family. While in the neonatal range, the meadow ecosystem is mainly composed of prickly rose (*Rosa acicularis*), wild red raspberry

(*Rubus idaeus*), fly honeysuckle (*Lonicera villosa*), and bluejoint grass (*Calamagrostis canadensis*).

Study design

We assessed bison diet and forage characteristics based on data collected in spring and summer for 2018, 2019, 2020, and 2023. For the core range from 2018 to 2020, we selected random female bison locations from GPS telemetry data, as well as random sites, focusing on the area from Ronald Lake in the north to the southern extent of the herd's range (Hecker et al., 2023). In 2023 we sampled the neonatal range using a stratified random design to select locations based on their relative position to the meadow complex and their relative intensity of use determined by the history of GPS telemetry locations since intensity of use in the area was high. We focused on the meadow complex as the number and concentration of GPS telemetry locations there was greatest. At each selected site in both ranges, we used a quadrat (0.0625-m^2) centered at confirmed bison locations (i.e., scat, foraged vegetation, bedding signs) or at the original coordinates if no bison sign was found to collect data on bison diet, forage biomass and macronutrient content (see Appendix 1 for example photos of sampling protocol and study area).

GPS telemetry locations came from collar data from adult female wood bison captured and marked between 2013 and 2023 by Alberta Environment and Protected Areas. The procedures used to capture and collar bison were approved by the Alberta Wildlife Animal Care Committee (permits nos. 51244, 53893, 54723, and 55748). GPS radio collars were set to record locations every 90 minutes and animal locations were filtered for errors by removing locations with low accuracy (dilution of precision > 5; Bjorneraas et al., 2010) and where individuals moved beyond the range a bison can move in a 90-minute interval.

Seasonal diet content

During 2018, 2019 and 2023, fresh scat samples were collected in a 15-m radius around each quadrat. If multiple scat samples were found at a site, only one was collected to avoid over representing the site location. Scat samples were classified as fresh based on odor, consistency and appearance, and collected in sealed 50-mL plastic vials. During the field seasons, scat samples were kept in cool, dark areas at the camping site and subsequently stored at -20 °C in a lab at the end of each season. Then, composite samples were created by combining ~5-mL of fecal material subsampled from three to five individual samples randomly selected for each year. This process was repeated ten to twelve times without replacement of fecal samples and final composite samples were sent to Jonah Ventures (Boulder, USA) for diet content analysis using DNA metabarcoding (see Appendix 2a for details).

Composite samples were analyzed for plant DNA via sequencing of the chloroplast *trn*L intron, a reliable approach to describe herbivore diets when short DNA fragments are present in degraded samples (Valentini et al., 2009, Craine et al., 2015). DNA sequences found in the samples were clustered into operational taxonomic units (hereafter taxonomic units) by using the Basic Local Alignment Search Tool (BLAST) from the National Center for Biotechnology Information (Blaxter et al., 2005; NCBI, 2023). BLAST identifies regions of similarity by comparing nucleotide sequences from samples with sequences of known organisms in its database (NCBI, 2023). We grouped taxonomic units based on their similarity (>97%) and their geographical distribution, considering only taxa that were known to be present in the area. When two or more species presented the same percent of similarity for a single sequence and were known to be present in the area, we used the higher taxonomic level (i.e., genus or family). Using the number of times each sequence was read within each sample, we then calculated the relative read abundance (RRA) for each taxonomic unit as the read count of that unit divided by the total number of reads across all taxonomic units (Deagle et al., 2018; Hecker et al., 2021). RRA represents the percentage of DNA belonging to each taxonomic unit and is used as a reliable proxy of the relative consumption of each item (Deagle et al., 2018). Only taxonomic units that accounted for at least 1% of the diet were included. Additionally, taxonomic units were categorized into four functional groups to identify dietary shifts throughout the year: graminoid (grasses and sedges), forb (herbaceous plants), browse (shrubs and trees), and other (see Appendix 2b for details).

Forage quantity and quality analyses

We quantified forage within each 0.0625-m^2 quadrat deployed at confirmed bison locations or original coordinates of selected sites. Within a 3-dimensional space above each quadrat, the foliar portion of all plant species were clipped from ground level to 2-m above ground, given that two meters is the maximum foraging height for an adult bison, and individual samples were stored in breathable paper bags in a meshed enclosure to allow airflow and drying. The samples were later transported to a lab to be dried at 60° C for 24 hours and weighed to measure dry biomass by species. Forage quantity was based on the dry biomass from plant species clipped inside each quadrat. To assess the forage quality, 20-g samples from the most frequently found plant species at each range were analyzed for chemical nutritional content at Nutrilytical Lab (Calgary, Canada). Information regarding crude protein and metabolizable energy (ME) was obtained for each species and an overall value for these nutritional components was then calculated for each quadrat. Crude protein values were converted to g/m^2 for better comparison and ME was expressed as Mcal/g.

Forage quantity and quality analyses were based only on plant species comprising at least 1% of the herd's diet throughout the year, and these species were grouped in one of three forage categories: shrubs, forbs and graminoids. Additionally, only sites surveyed between 1 June and 15 July were included, because they represent the peak of vegetation green-up in the area and coincide with the time when the herd is in their neonatal range (see Appendix 2c, 2d for details). Due to the non-normal distribution of the data, differences between the herd's neonatal and core range for all forage groups were determined using non-parametric Mann-Whitney-Wilcoxon tests. All data organization and analysis were performed using the software R 4.1.0 (R Core Team, 2021).

Results

Seasonal diet content

A total of 122 bison scat samples were collected during 2018, 2019, and 2023. Of that total, 91 samples (74.6%) were from the core range representing the winter (pre-migration) and mid-late summer (post-migration) diet, while 31 samples (25.4%) were from the neonatal range representing the late-spring/early-summer migration diet. The DNA analysis detected 386 unique sequence variants across all samples (seasons), but 73 less common variants were excluded due to being absent in the study area. This resulted in 58 unique taxonomic units for winter, 40 unique taxonomic units for late-spring/early-summer, and 59 unique taxonomic units for mid-late summer with an overall cumulative read count of ~96%.

The herd's winter diet in the core range was composed of browse items (49.8%), followed closely by graminoids (44.6%), then forbs (3.5%), and other groups (2.1%). The three taxonomic units with the highest RRA values were *Carex* spp. (RRA = 19.6, SE = 4.5), *Viburnum edule* (RRA = 18.3, SE = 5.6), and *Sparganium* spp. (RRA = 17.1, SE = 8.7) (Figure 2b). The herd's late-spring/early-summer diet in the neonatal range was dominated by browse items (84.8%), followed by forbs (12.9%), and then other groups (2.2%) and graminoids (0.1%). Two shrub species, *Rosa acicularis* and *Rubus idaeus*, were the most prevalent, with an RRA of 71.2 (SE = 6.5) and 8.4 (SE = 1.5) respectively, followed by the forb *Persicaria amphibia* at 5.0 (SE = 4.9) (Figure 2b). The herd's mid-late summer diet in the core range was dominated by browse (60.2%), followed by forbs (36.5%), other groups (2.8%) and graminoids (0.5%). *Rosa acicularis* had the highest RRA (RRA = 42.1, SE = 2.6), followed by *Chamaenerion angustifolium* (RRA = 24.3, SE = 2.2), and *Ribes triste* (RRA = 7.4, SE = 1.9) (Figure 2b; see Table 1 for details). Overall, we found strong seasonal changes in the herd's diet, going from a more graminoid-dominated diet in winter, to a shrub and forb-dominated diet in late spring and through the summer (Figure 2a). It was notable that browse was the most dominant component of the herd's diet in their neonatal range during a period when browse items are exhibiting new spring growth.

Forage quantity

Forage quantity was quantified across 348 sites (plots), of which 217 were in the core range and 131 in the neonatal range (see Appendix 3 for detailed distribution of plots). The neonatal range had significantly higher biomass of shrubs ($p \leq 0.01$) and forbs ($p \leq 0.001$), with median values of 71.20-g/m^2 (SE = 10.77) for shrubs and 41.04- g/m^2 (SE = 11.51) for forbs. Conversely, graminoids were significantly more abundant ($p \leq 0.001$) in the core range at a median dry biomass of 8.80- g/m^2 (SE = 7.18), approximately 18 times greater than in the neonatal range. Shrub and forb biomass were 1.7 and 3.8 times higher, respectively, in the neonatal range compared to the core range (Figure 3a; details can be found in Appendix 4).

Forage quality

We quantified forage quality from 228 sites, of which 97 were from the core range and 131 were from the neonatal range (see Appendix 4 for detailed distribution of plots). Crude protein was significantly higher for shrubs ($p < 0.001$) and forbs ($p < 0.001$) in the neonatal range compared to the core range, being 2.7 and 3.2 times higher for shrubs (median = 10.11-g/m^2, SE = 1.73) and forbs (median = 6.05-g/m^2, SE = 1.89), respectively (Figure 3b). While the core range had the highest crude protein for graminoids ($p < 0.001$), being ~46 times higher than the neonatal range (median = 1.53-g/m^2, SE = 1.98). The neonatal range also had highest amount of ME for shrubs ($p < 0.001$) and forbs ($p < 0.001$), being 3.0 (median = 0.01 Mcal/g, SE = 0.16 e-02) and 3.7 (median = 0.01 Mcal/g, SE = 0.18 e-02) times higher, respectively. However, the core range had higher ME for graminoids ($p < 0.005$), being 36 times higher than the neonatal range (median = 0.14 e-02 Mcal/g, SE = 0.06 e-03) (Figure 3c; details can be found in Appendix 6).

Discussion

Our findings reveal a clear shift in the RLBH's diet between the ranges, as initially hypothesized. During winter in the core range, the herd primarily consumed graminoids and shrubs. However, in late spring and early summer in the neonatal range, their diet shifted predominantly to shrubs. By mid to late summer, as they returned to their core range, the diet was balanced between shrubs and forbs (Figure 2a). We suggest that the shifting seasonal pattern was primarily due to the temporal and spatial availability of forage. In winter, when graminoids constituted a big component of the herd's diet, forage options were limited due to the absence of green foliage. After snowmelt and the emergence of spring, the new growth of shrubs and forbs became available for bison (Hartley & Jones, 1996). The composition of available forage also differed between ranges, with the core range containing numerous wetlands that are rich in graminoid forage, while the neonatal range is dominated by upland ecosystems that are much lower in abundance of graminoids. This dietary shift also indicated a change in foraging behavior, transitioning from a more grazing-dominated behavior in winter, to a browsing-dominated behavior in spring and summer, supporting previous findings on bison (Bergmann et al., 2015; Leonard et al., 2017; Hecker et al., 2021).

Our results also supported our hypothesis regarding forage quantity and quality between ranges, for shrubs and forbs. The neonatal range presented the highest values of biomass, crude protein and ME for these forage types, while biomass, crude protein and ME for graminoids were higher in the core range. These discrepancies in the quantity and quality of forage can be attributed to the different ecosystems between ranges. The neonatal range is predominantly composed of upland deciduous forest and upland meadows, which are rich in forbs and shrubs, whereas the core range is characterized by ecosystems abundant in graminoid vegetation. Although graminoid forage is rich in fiber, it contains lower amounts of protein and energy compared to shrubs and forbs (Lee, 2018). Additionally, the neonatal range features an extensive and continuous upland shrubby meadow, unique in the herd's range, dominated by the plant species prickly rose and raspberry, which were the two most abundant species in the herd's diet in the neonatal range. Prickly rose also emerged as the primary dietary species in the core range during mid and late summer (Figure 2b). These species are of high nutritional value, with prickle rose presenting the highest ME (2.78 Mcal/kg) and raspberry ranking among the top three species with highest crude protein (19.8%) among all shrub species evaluated in the neonatal range (Appendix 7).

It is no surprise that the range with higher biomass for a specific forage type, also showed higher crude protein and ME in that forage type as it is directly related to the biomass of each forage item at that site. However, we found that the magnitude of the differences between ranges in quality was not directly explained by the quantity of forage. For instance, shrub biomass in the neonatal range was 1.7 times greater than in the core range, but its crude protein and ME content was 2.7 and 3.0 times higher, respectively, than in the core range (Appendix 4 and 6). Similarly, forb biomass in the neonatal range was 3.8 times greater, but its crude protein and ME were 3.2 and 3.7 higher, respectively, than in the core range. Given that ME and crude protein are critical for calf growth and overwinter survival (Cook et al., 2004; Tollefson et al., 2011), these results suggest that forage quality, particularly of shrubs, plays a more crucial role than quantity in the herd's migration during their neonatal period. Our results support previous studies reporting that herbivore migrations are primarily influenced by forage quality, especially when animals are under energetic stress (Hebblewhite, 2008; Cagnacci et al., 2011; Merkle et al., 2016).

Tracking the phenological waves of the highly nutritious new forage, a concept coined as the greenwave hypothesis, has received empirical support as being one of the best explanations for the timing and extent of migratory movements in ungulates (Van Soest, 1982; Bischof et al., 2012; Aikens et al., 2017). However, various responses in how animals track new forage have been documented, with populations surfing the greenwave (Aikens et al., 2017; Sigrist et al., 2022), others jumping it and arriving at their final summer ranges (Bischof et al., 2012; Laforge et al., 2020), and in some cases, ungulates even manipulate the greenwave through intense foraging (Geremia et al., 2019). In our study we did not directly evaluate the strategy that the RLBH uses to track new growth, but a previous study found that it is unlikely that the herd is surfing the greenwave (Hecker, 2022). The spatial variation in phenology associated with terrain between the core and neonatal range is minimal due to its low relief and the distance traveled between ranges is not far enough to substantially alter phenology. Further studies are needed to better understand how the herd tracks the new growth to maximize their energy intake, but broadly speaking green-up occurs at the same time between the core and neonatal range suggesting it has less to do with phenology than quantity and quality of forage.

Our study focused on the influence of forage characteristics on the herd's migration, but other factors may also play an important role in explaining the herd movements. In many cases, ungulates migrate to seasonal ranges to reduce predation risk for themselves or their calves (Festa-Bianchet et al., 1988; Fryxell and Sinclair, 1988; Hebblewhite and Merrill, 2007). Consequently, predator pressure could be influencing the RLBH migration. Wolves and black bear (*Ursus americanus*) are the only species within the herd's range that could prey on bison or their calves. Wolves, considered the primary predators of bison in North America, can exert top-down control on bison populations, including those in Wood Buffalo National Park just north of Ronald Lake (Joly and Messier, 2004). Although black bears are not the main predators of bison due to their size and omnivorous diet, there is evidence that they opportunistically prey on other ungulates and their calves (Bowersock et al., 2021; Bonin et al., 2023). Previous studies on wolves and black bears have shown limited predation pressure on the RLBH (Dewart, 2023; Sharp et al., 2024), although predators could influence the herd's migration indirectly. By aggregating in larger numbers or moving to areas where predation risk is perceived to be lower, individuals can spend less time being vigilant and more time foraging (Xinming et al., 2007; Christianson and Creel, 2010). This is crucial for the herd, as females need to meet their higher nutritional requirements while simultaneously protecting their neonates from possible predators.

Insect harassment is another possible factor influencing the herd's migration during this time of the year. Biting insects have been shown to directly affect ungulate foraging behaviors and habitat selection, including that of bison (Hagemoen and Reimers, 2002; Witter et al., 2012;

Belanger et al., 2020). Insect harassment can have adverse fitness consequences due to the increased nutritional demands associated with reduced food intake and the increase of avoidance behaviors (Fitze et al., 2004; Benedict and Barboza, 2022; Johnson et al., 2022). This is especially true for calves, as evidence shows that insect harassment can affect their weight and survival (Weladgi et al., 2003; Johnson et al., 2022). Some of the most common ectoparasitic insects in boreal forests, including the families Simuliidae, Culicidae, and Tabanidae, use wetlands as breeding grounds (Lewis, 1987), which are prevalent in the core range of the RLBH. Thus, insect harassment may help explain the herd's movements to the neonatal range, further supported by our findings that their diet is dominated by graminoids during winter, when insect harassment is absent, and decreases during spring and summer (Figure 2a).

Apart from the factors not considered here that could also influence the herd's migration and diet, we acknowledge that our study also presents some limitations. First, our diet results come from a DNA metabarcoding approach, which infers diet from the proportion of sequence reads recovered from fecal material. This semi-quantitative method can introduce bias due to differential digestion of food taxa and, which may not always accurately reflect the actual proportion of consumed plants (Nakahara et al., 2015; Deagle et al., 2018). The differential digestion of food taxa, combined with DNA degradation after ingestion, likely explains the presence of a high number of sequence variants (i.e., 73) that did not match any known plant species in the area.

Second, it is important to note that our quantity and quality estimates are based on data from sites visited after they were utilized by bison, leading to an underestimation of the actual availability at the time of utilization. Additionally, our findings may also be influenced by the effect of foraging on vegetation regrowth. Browsed shrubs and forbs are likely to exhibit lower quality compared to unbrowsed individuals, while grazed graminoids may offer higher nutritional value than their ungrazed counterparts. These effects of browsing and grazing on forage quality likely amplify the differences already observed between the neonatal and core range.

Conclusions

Our study provides valuable insights into factors influencing the migration of the RLBH. We found a clear shift in the herd's diet between its core and neonatal ranges, with a heavily browse-dominated diet in late spring and early summer when the herd occupies the neonatal range with their young calves. Our results suggest that this diet shift in the neonatal range is influenced by the higher quantity and quality of forbs and shrubs items that this range offers in comparison to the core range, with forage quality possibly playing an even more significant role than quantity in the range selection during their neonatal period. While other factors not considered here may also influence the herd's migration, our results indicate a link with forage quantity and quality, which also aligns with the higher nutritional requirement that female bison are experiencing during this time of the year. This study is crucial for identifying critical habitat for bison during a period when they are nutritionally vulnerable. This is particularly important for this herd, as its range is close to areas of oil sand exploration and development and its conservation has significant ecological and cultural implications.

Tables

Table 1. Identified taxonomic units for all seasons with their six-letter species code used for RRA analysis.

Taxonomic unit	Family	Genus	Species	Forage group	Mean Relative Read Abundance (RRA)		
					Winter	Late spring	Mid-late summer
AMEALN	Rosaceae	*Amelanchier*	*alnifolia*	Browse	7.7	-	-
CARSPP	Cyperaceae	*Carex*	NA	Graminoid	19.6	-	-
CHAANG	Onagraceae	*Chamaenerion*	*angustifolium*	Forb	-	4.5	24.3
CORCAN	Cornaceae	*Cornus*	*canadensis*	Forb	-	-	1.3
CORSER	Cornaceae	*Cornus*	*sericea*	Browse	13.9	3.0	-
EQUSPP	Equisetaceae	*Equisetum*	NA	Other	-	2.1	1.5
LATPAL	Fabaceae	*Lathyrus*	*palustris*	Forb	-	-	2.4
LYCANN	Lycopodiaceae	*Lycopodium*	*annotinum*	Other	-	-	1.5
OENBIE	Onagraceae	*Oenothera*	*biennis*	Forb	-	-	4.4
PERAMP	Polygonaceae	*Persicaria*	*amphibia*	Forb	1.2	5.0	2.9
POAFAM	Poaceae	NA	NA	Graminoid	3.1	-	-
POTNOR	Rosaceae	*Potentilla*	*norvegica*	Forb	-	1.4	-
POPTRE	Salicaceae	*Populus*	*tremuloides*	Browse	3.7	-	-
RIBTRI	Grossulariaceae	*Ribes*	*triste*	Browse	-	-	7.4
ROSACI	Rosaceae	*Rosa*	*acicularis*	Browse	-	71.2	42.1
RUBIDA	Rosaceae	*Rubus*	*idaeus*	Browse	-	8.4	-
SALSPP	Salicaceae	*Salix*	NA	Browse	5.7	-	5.4
SPASPP	Sparganiaceae	*Sparganium*	NA	Graminoid	17.1	-	-
SPHSPP	Sphagnaceae	*Sphagnum*	NA	Other	1.4	-	-
TYPLAT	Typhaceae	*Typha*	*latifolia*	Graminoid	1.1	-	-
VACSPP	Ericaceae	*Vaccinium*	NA	Browse	-	-	1.2
VIBEDU	Caprifoliaceae	*Viburnum*	*edule*	Browse	18.3	-	-

Note: The symbol - indicates taxonomic units that constitute at least 1% of a seasonal diet but are not present in that specific season.

Figures

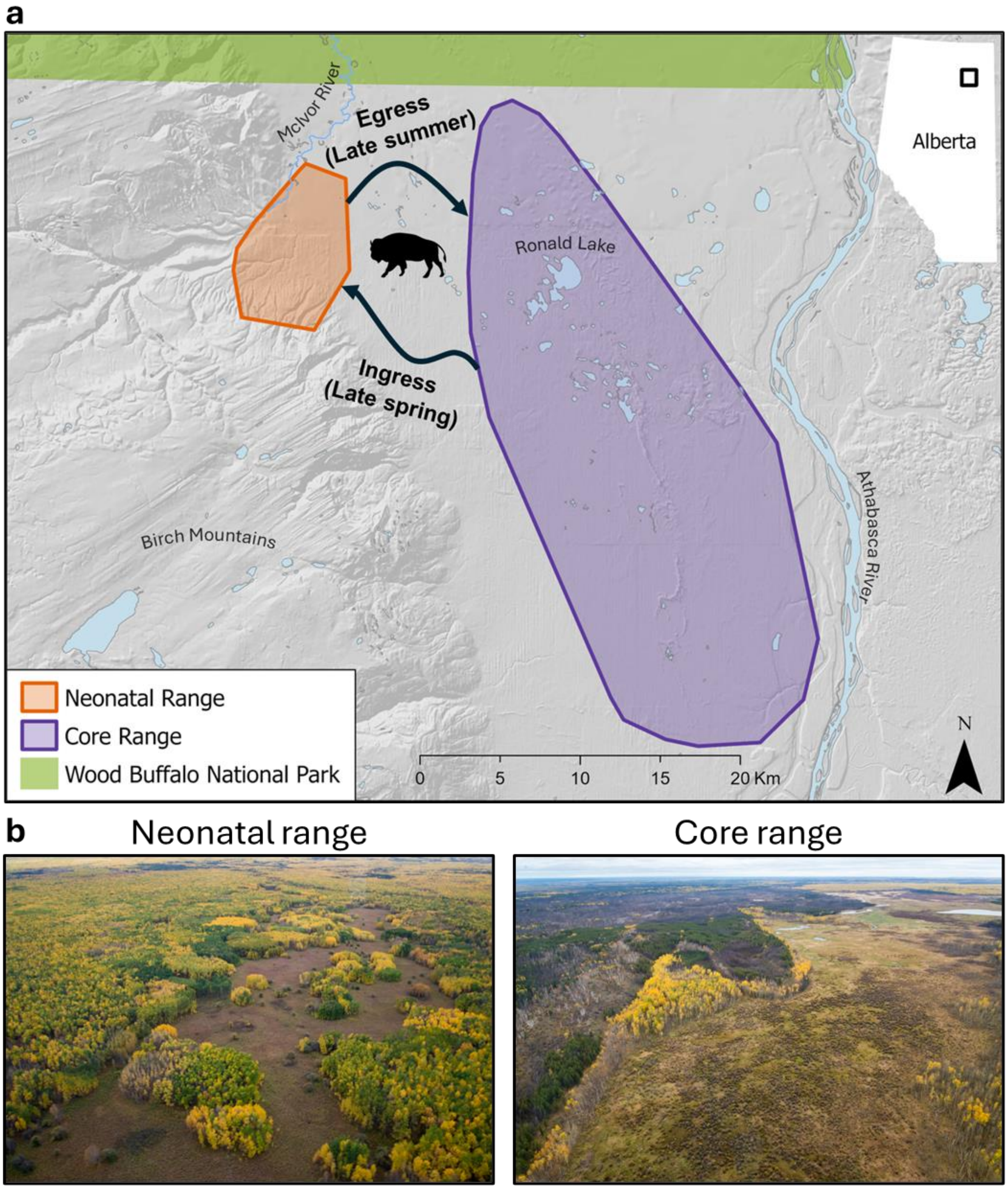

Figure 1. Ronald Lake wood bison herd study system in northeastern Alberta, Canada. Generalized maps of the herd's ranges and movements (a), and aerial photographs (source: S. Nielsen) of the two ranges illustrating the representative conditions during early fall (b).

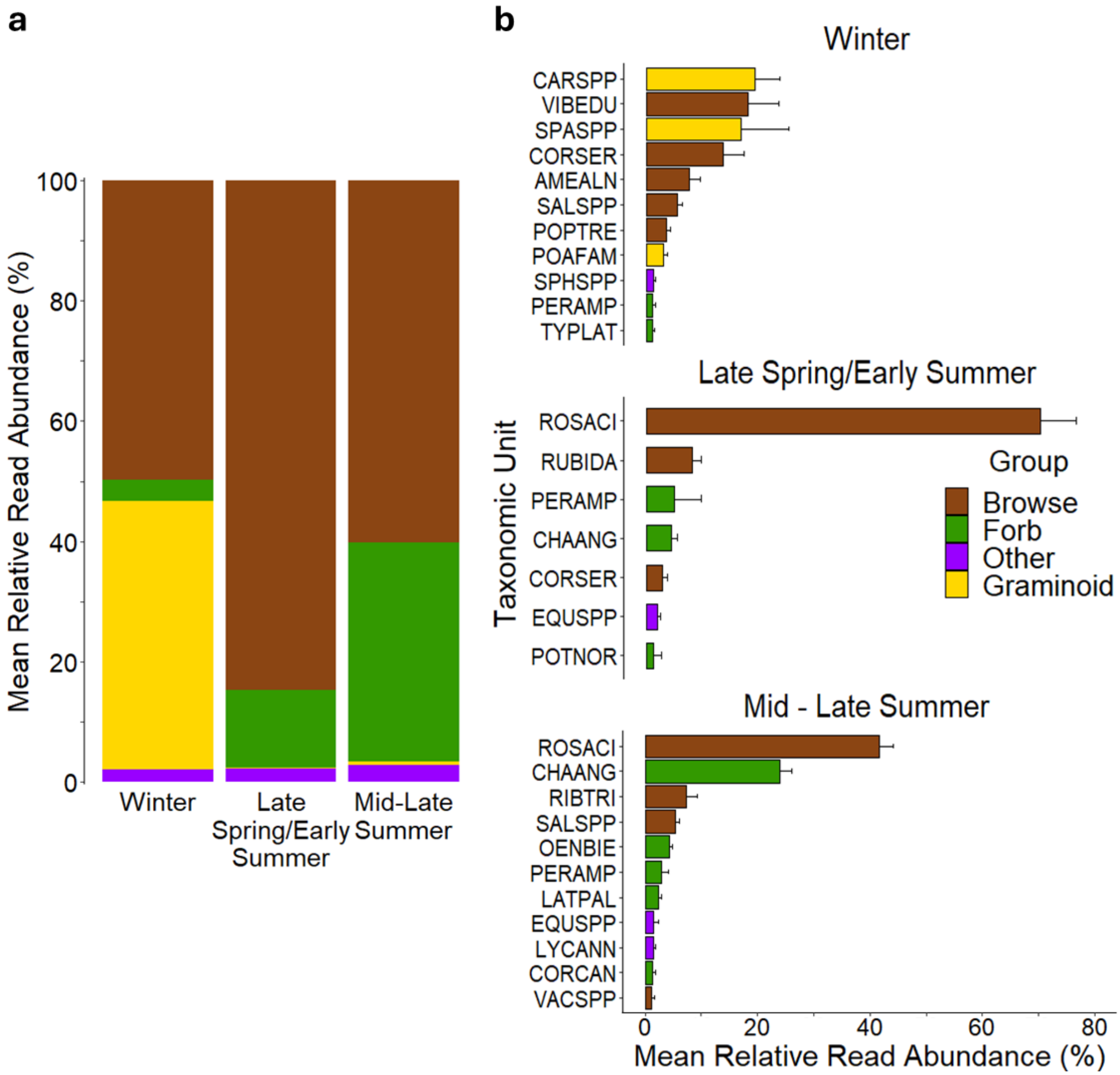

Figure 2. Seasonal dietary contribution of forage groups for the Ronald Lake wood bison herd (a) and seasonal diets with taxonomic units that represent at least 1% of the diet identified as six-letter species codes of family, genus, or species (see Table 1 for details) (b).

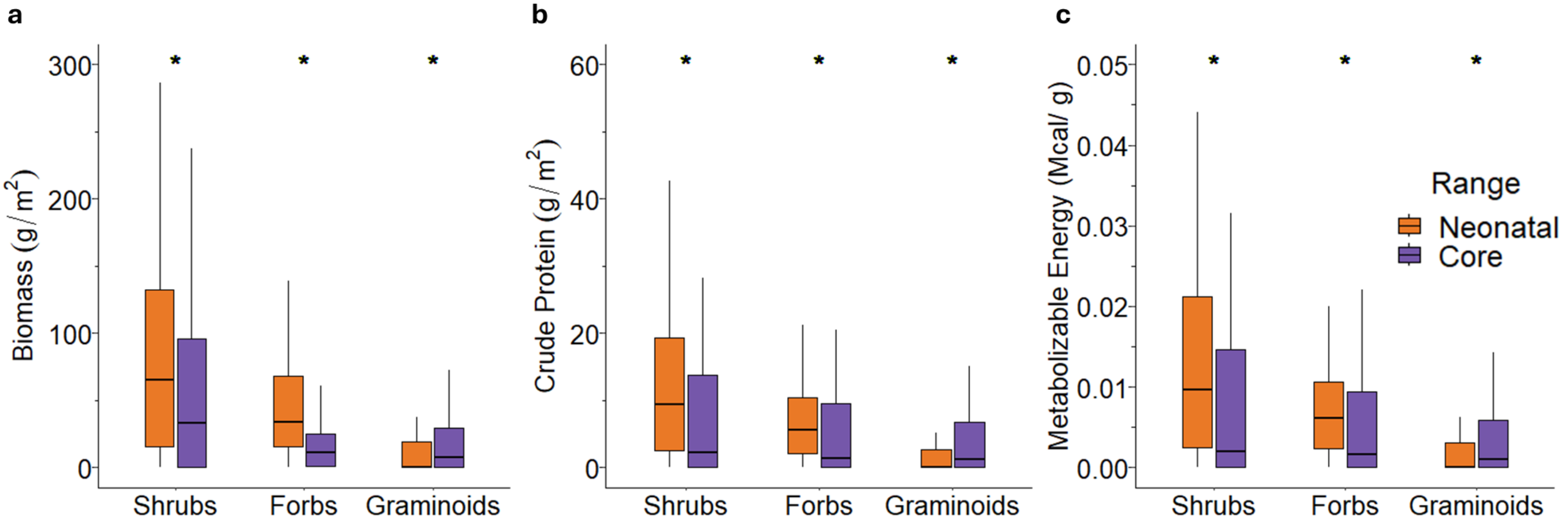

Figure 3. A comparison of dry biomass (a), crude protein (b), and metabolizable energy (c) between the neonatal and core ranges of the Ronald Lake Bison Herd for shrubs, forbs and graminoids. The symbol * represents significant ($p < 0.01$) differences between the two ranges based on Wilcoxon tests.

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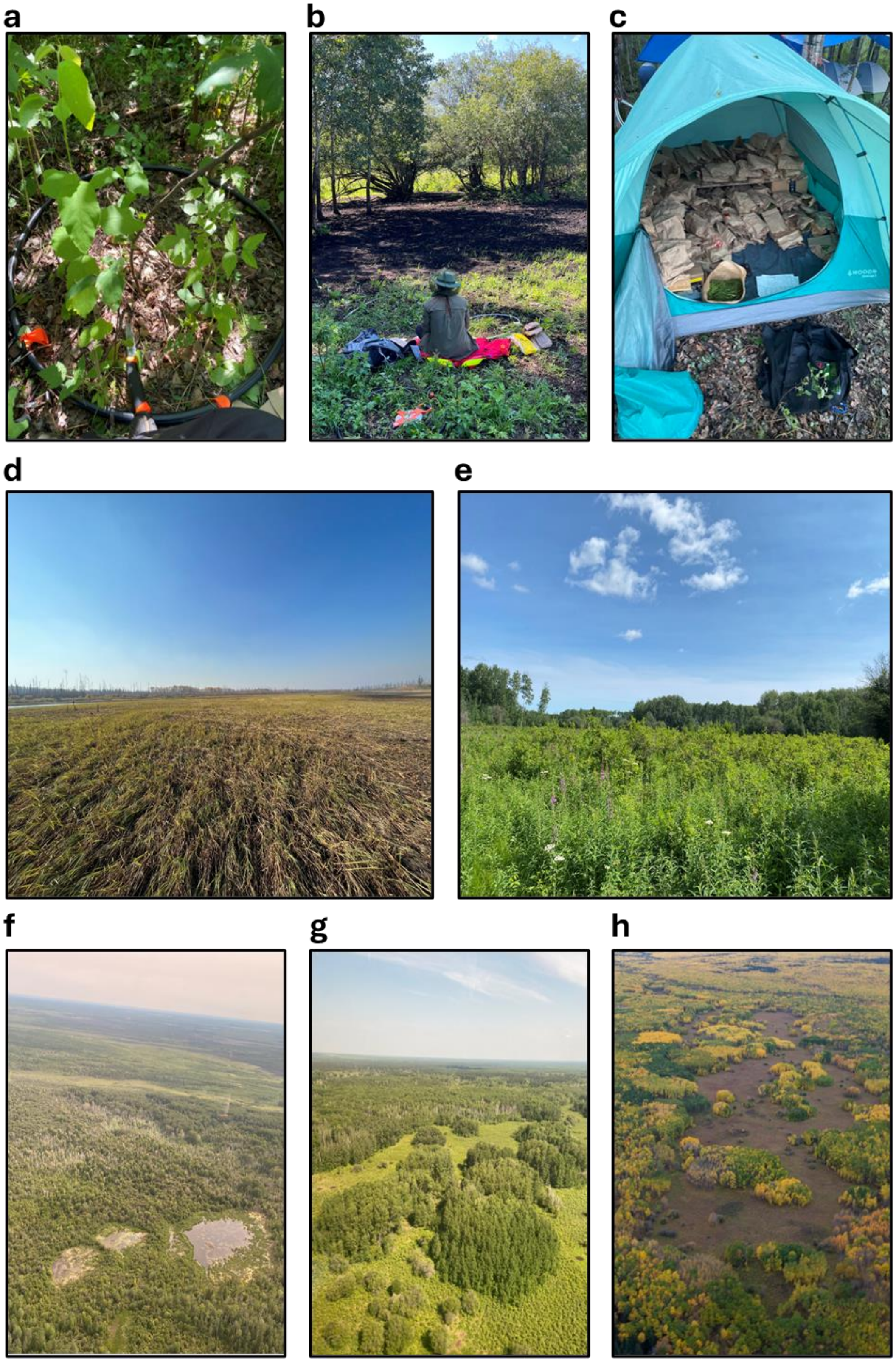
Appendices

Appendix 1. Sampling process and field photos in the Ronald Lake wood bison herd ranges. Circular quadrat (0.0625-m^2) used to clip vegetation (a); field technician collecting information in a wallow area in the neonatal range (b); on-site storage of clipped vegetation samples (c); graminoid wetland in the core range (d); shrubby meadow complex in the neonatal range (e); summer aerial view of the core range (f); summer aerial view of the meadow complex in the neonatal range (g); and fall aerial view of the meadow complex in the neonatal range (h).Photographs a, c, e, and f were taken by Ivy Boddez; b was taken by Garrett Rawleigh; d was taken by Darren Epperson; g was taken by Amber Harris; and h was taken by Scott Nielsen.



Appendix 2. Detailed methods for composite samples creation (a), seasonal diet content (b), and forage quantity (c) and quality (d) analyses.

a. If multiple samples were found around a site, only one fresh sample was collected to avoid over representing a location or individual. In the core range, scat samples were collected only around sites of known bison locations that were visited within 10-days of the bison presence. Each site was visited only one time. Composite samples were created by randomly selecting three to five individual fecal samples per season from the same year, and this process was repeated 10 times for winter and late summer seasons in the core range, and 12 times for late spring/early summer in the neonatal range. Composite samples were first created for the scat collected in 2018 and 2019, and the same process was applied to the 2023 samples to maintain consistency in the design.

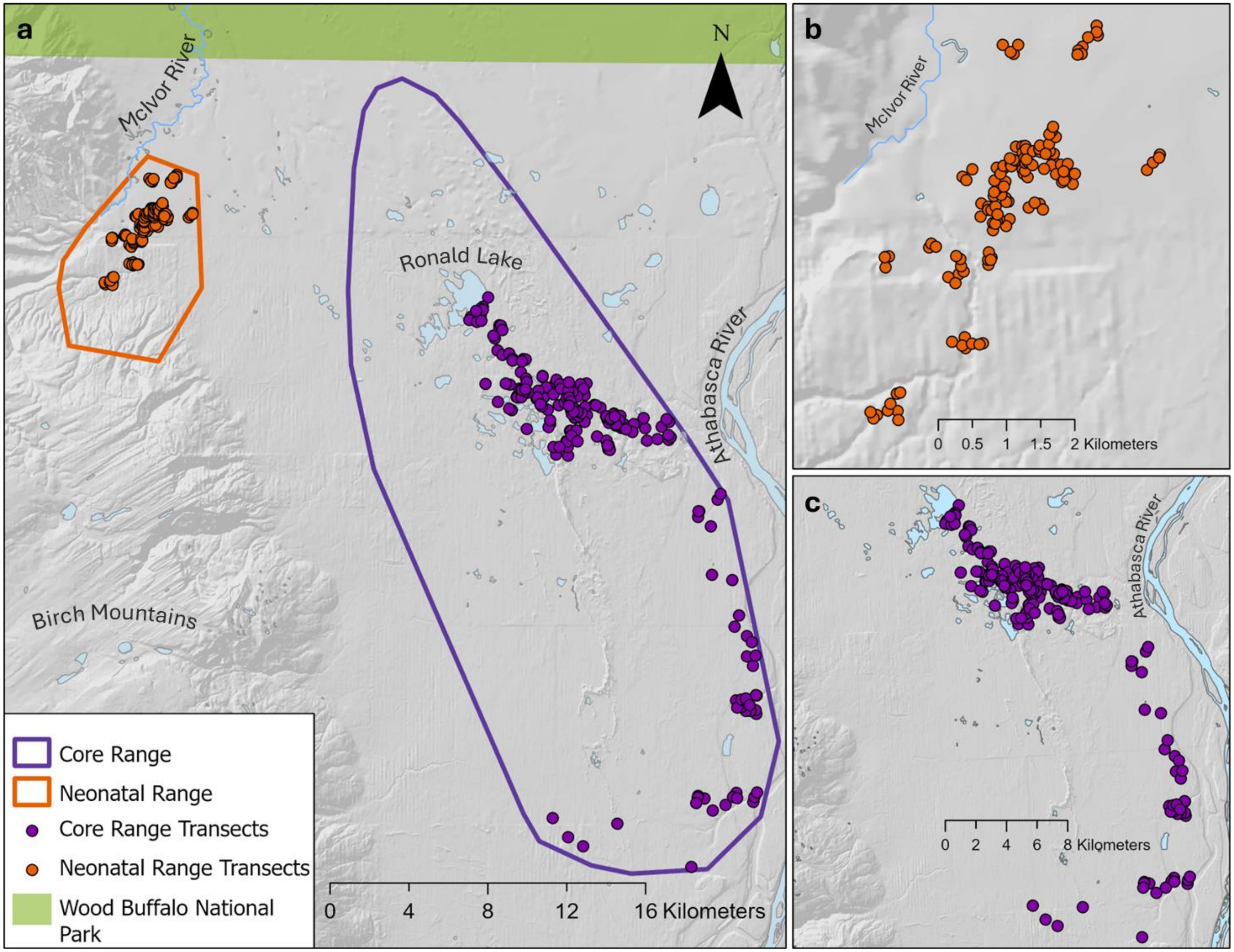
b. Taxonomic units' assignment of unique sequence variants found in the scat composite samples was based on the known distribution of plant species. This distribution was determined based on the book "Plants of the Western Forest: Alberta, Saskatchewan & Manitoba. Boreal and Aspen Parkland" (Johnson et al., 2020) and public from the iNaturalist database (https://www.inaturalist.org/). Only plant species documented to be present in the boreal forest in the northern part of the province were considered for taxonomic unit's assignment.

When two or more species presented the same percent of similarity for a single sequence and were known to be present in the area, the higher taxonomic unit (i.e., genus or family) was used. However, an exception was made for some sequences found in composite samples representing the late-spring/early-summer diet in the neonatal range. These sequences accounted for 199550 number of reads (~72% of the total reads for that season) but could not differentiate between the species prickly rose (*Rosa acicularis*), woodland strawberry (*Fragaria vesca*), and virginia strawberry (*Fragaria virginiana*), all of which are present in the area but vary dramatically in their abundance (*Fragaris spp.* being less common). Ultimately, these sequences were assigned to *Rosa acicularis* (ROSACI). Field data indicated that prickly rose was the most prevalent between these species in the neonatal range, being found in ~79% of sampled sites, with a collected biomass of 529.9-g. In contrast, the combined presence of strawberry species (which would not be distinguished from each other in the field) was found in only ~12% of plots, with a collected biomass of 14.0-g..

c. Biomass values were based on clipped vegetation of the foliar portion for all plant species found in each quadrat. However, only species comprising at least 1% of the herd's diet in any season, based on seasonal diet content results, were included in the analysis. Moss species (i.e. *Sphagnum* spp.) were excluded from biomass estimation. The total biomass for each plant species was calculated per quadrat and then categorized into shrubs, forbs, and graminoids. Each quadrat had an area of 0.0625-m^2, hence all biomass values were divided by 0.0625 to represent values in g/m^2.

d. Macronutrient (i.e., protein and ME) analysis followed the same steps taken for the biomass analysis. Protein values were originally obtained as the percentage of the total dry biomass per plant species, it was necessary to multiply this percent by the biomass of each species per quadrat to determine the total protein content. ME values, originally expressed in Mcal/kg (i.e., Megacalories per kilogram), were divided by 1000 and then multiplied by the total biomass of each plant species per quadrat to obtain a final value of Mcal/g (i.e., Megacalories per gram).

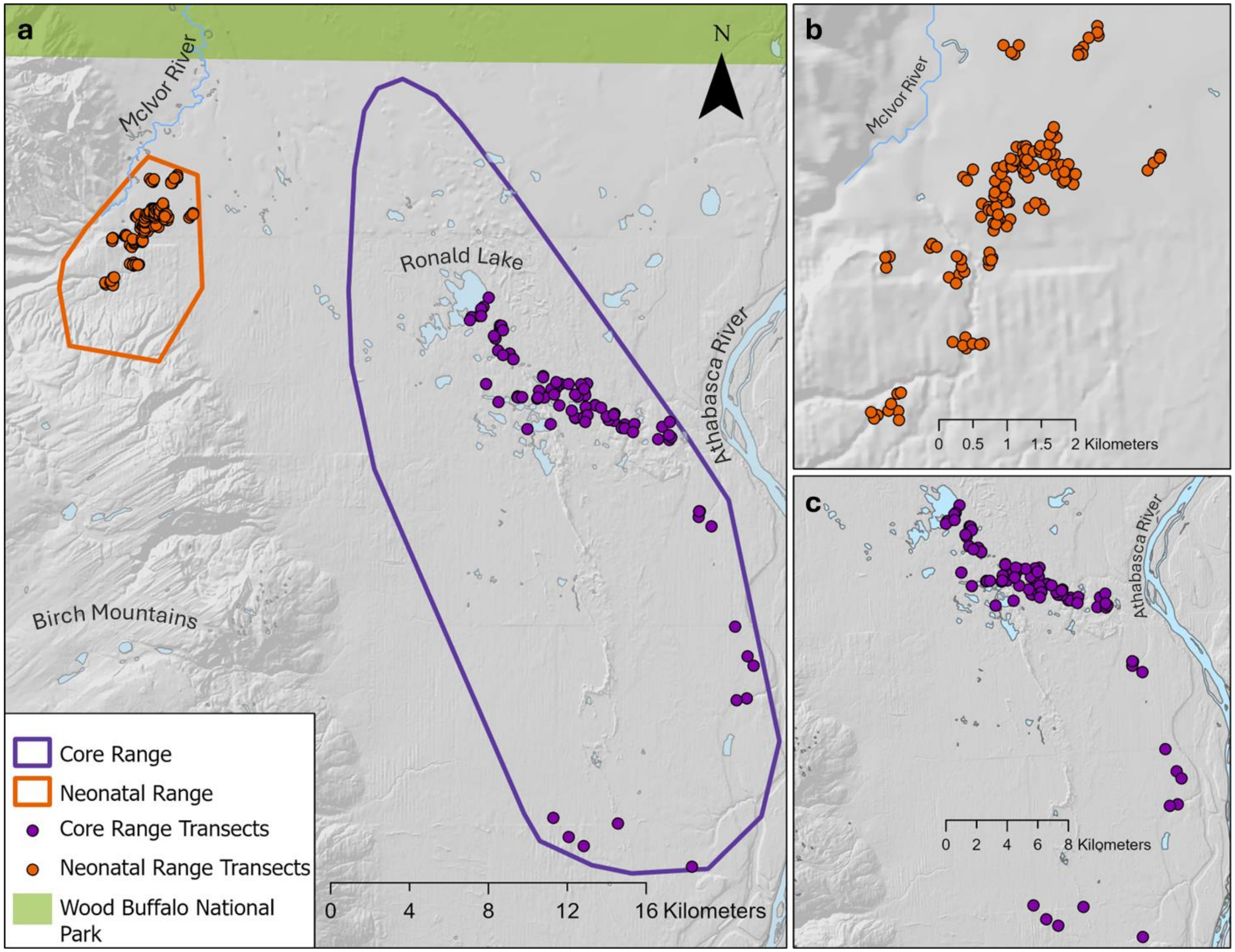
Appendix 3. Distribution of sampled sites for biomass analyses in the Ronald Lake wood bison herd ranges (a), with a more detailed view of the 131 sites in the neonatal range (b) and the 217 sites in the core range (c) shown.



Appendix 4. Biomass median values, standard errors (SE), and Wilcoxon test p-values between ranges and forage groups.

Forage item	Range	Biomass (g/m2)	SE	P-value
Shrub	Core	41.12	14.45	≤ 0.01
	Neonatal	71.20	10.77	
Forb	Core	10.88	2.19	≤ 0.001
	Neonatal	41.04	11.51	
Graminoid	Core	8.80	7.18	≤ 0.001
	Neonatal	0.50	3.51	

Appendix 5. Distribution of sampled sites for macronutrient analysis in the Ronald Lake wood bison herd ranges (a), with a more detailed view of the 131 sites in the neonatal range (b) and the 97 sites in the core range (c) shown.



Appendix 6. Protein and ME median values, standard errors (SE), and Wilcoxon test p-values between ranges and forage groups.

Forage item	Range	Protein (g/m2)	SE	P-value	ME (Mcal/g)	SE	P-value
Shrub	Core	3.77	2.96	≤ 0.001	0.36 e-02	0.26 e-02	≤ 0.001
	Neonatal	10.11	1.73		0.01	0.16 e-02	
Forb	Core	1.87	1.53	≤ 0.001	0.18 e-02	0.15 e-02	≤ 0.001
	Neonatal	6.05	1.89		0.01	0.18 e-02	
Graminoid	Core	1.53	1.98	≤ 0.001	0.14 e-02	0.19 e-02	≤ 0.005
	Neonatal	0.03	0.49		0.38 e-04	0.06 e-03	

Appendix 7. Protein and ME raw values for the most frequent plant species in the neonatal range.

Plant species	Forage item	Protein (%)	ME (Mcal/kg)
Ribes spp.	Shrub	20.7	2.2
Rubus idaeus	Shrub	19.8	2.6
Aralia nudicaulis	Shrub	15.1	2.1
Prunus spp.	Shrub	15.1	2.1
Viburnum opulus	Shrub	14.0	2.1
Lonicera ivolucrata	Shrub	13.1	2.4
Cornus sericea	Shrub	12.2	2.7
Rosa acicularis	Shrub	11.4	2.8
Salix spp.	Shrub	9.1	1.3
Poaceae family	Graminoid	14.7	2.3
Carex spp.	Graminoid	12.4	2.1
Vicia sativa	Forb	26.4	2.4
Urtica dioica	Forb	25.8	2.3
Epilobium spp.	Forb	22.2	2.6
Lathyrus spp.	Forb	20.8	2.3
Geum rivale	Forb	20.1	2.4
Dracocephalum parviflorum	Forb	18.8	2.0

Viola spp.	Forb	18.1	2.2
Martensia paniculata	Forb	18.0	1.8
Prosartes spp.	Forb	18.0	1.6
Thalictrum venulosum	Forb	17.8	2.4
Galium spp.	Forb	15.6	2.1
Equisetum spp.	Forb	15.5	2.0
Lilium spp.	Forb	14.5	2.4
Mitella diphylla	Forb	13.2	2.4
Cornus canadensis	Forb	9.8	2.6
Gaultheria spp.	Forb	9.4	2.6
Linnaea borealis	Forb	6.1	2.1